

POLYPHENISM AND POPULATION BIOLOGY OF *EUREMA ELATHEA* (PIERIDAE) IN A DISTURBED ENVIRONMENT IN TROPICAL BRAZIL

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ABSTRACT. A population of *E. elathea* was studied for 13 months, from May 1996 to May 1997 in a disturbed environment in suburban Campinas, southeastern Brazil. The population showed fluctuations in numbers throughout the study period, with well-marked peaks of abundance in June–July, November–December and February. Sex ratio was male biased in four months and the time of residence was higher in the dry season. Both sexes were polyphenic; paler phenotypes occurred in the dry season and darker phenotypes in the wet season. Paler phenotypes were more frequently recaptured and had higher residence values than darker ones. Differences in behavior were attributed to adaptation to seasonally different environments.

Additional key words: Coliadinae, mark-recapture, urban butterflies.

The recent surge of interest in the conservation of tropical environments has led to an increase in studies of the natural history and ecology of organisms residing in the tropics (Noss 1996). These have included some long-term studies on population biology of neotropical butterflies, focused mainly on aposematic groups such as Heliconiini, Ithomiinae and Troidini (Turner 1971, Ehrlich & Gilbert 1973, Brown & Benson 1974, Drummond 1976, Young & Moffett 1979, Brown et al. 1981, Saalfeld & Araujo 1981, Vasconcellos-Neto 1980, 1986, 1991, Freitas 1993, 1996, Haber 1978, Rogner & Freitas 1999). Population studies with the Pieridae, however, have focused on non-tropical species, especially agricultural pests (Watt et al. 1977, 1979, Tabashnik 1980) common in this family (Chew 1995).

Seasonal polyphenism (Shapiro 1976, 1984) is an interesting feature of some pierid butterflies (the “whites” and “small yellows”). Numerous insect groups, especially butterflies, are polyphenic in response to seasonal abiotic factors (Shapiro 1976). Degree of melanization, number of wing spots (especially eye-like markings on the wings in Satyrinae), and color variations have been attributed to adaptation to seasonally different environments and thermoregulation (Shapiro 1976, Brakefield & Larsen 1984, Kingsolver & Wiernasz 1987, Braby 1994, Van Dyck et al. 1997, Windig et al. 1994). In general, seasonal morphs are related to dry vs. wet season in the tropics, and spring vs. summer or fall in temperate regions (Nylin 1989). Many different environmental factors induce polyphenism (see Shapiro 1984 and Jones 1992). Different behaviors linked to different color patterns also have been reported (Shreeve 1987, Nakasuji & Nakano 1990, Van Dyck et al. 1997).

The pierid *Eurema elathea* (Cramer, 1777) is a small Neotropical butterfly common in lawns, pastures, and other disturbed environments (DeVries 1987, Brown

1992). The polyphenism in this species was reported by Brown (1992), who noted that dry season forms were dorsally paler than wet season forms. The species is common on the Campus of the Universidade Estadual de Campinas (Unicamp), where it can be observed flying on the lawns and visiting several species of wild flowers (Oliveira 1996).

This paper provides a detailed account of the population parameters of *Eurema elathea*, and our objectives are to: (1) examine the age-structure, size and sex ratio and size of the population; (2) describe the variation in proportions of the different polyphenic types throughout the year; and (3) provide subsidies to the management of this species in urban habitats.

MATERIALS AND METHODS

A mark-release-recapture (MRR) study was carried out on the Campus of the Universidade Estadual de Campinas (Unicamp), São Paulo state, southeastern Brazil, as part of a project of study of urban ecology on the Campus of the University. Annual rainfall is about 1360 mm and mean temperature 20.6°C (data from the Instituto Agrônômico de Campinas). The regional climate is markedly seasonal, with a warm wet season from September to April and a cold dry season from May to August. During the research, the mean temperature of the coldest month was 17.6°C and of the warmest month was 24.8°C, with climate typical of the region (Fig. 1), except for May 1997, which was a rainy month and thus was included in the wet season.

The vegetation on the campus where the study was conducted consists of large lawns with sparse trees and scattered small flowering shrubs. The lawn was mowed five times during the period of study, as part of normal procedures of maintenance of the campus. The study area was divided into nine plots corresponding to lawns separated by walking trails connecting the buildings on the Campus (Fig. 2).

Butterflies were marked and recaptured between 28 May 1996 and 27 May 1997 (1–3 times per week), in

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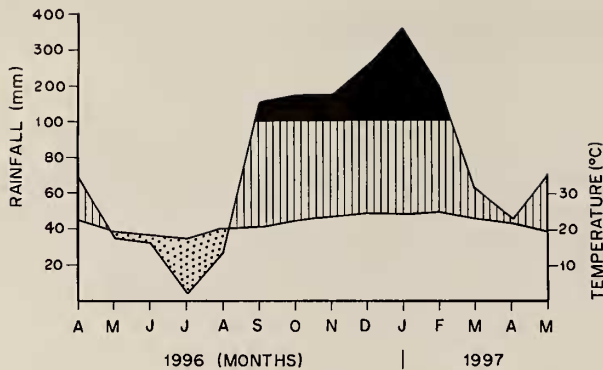


FIG. 1. Climagram for the Campinas region during the research (based on Santos 1965 and Walter 1985). Hatched = humid periods, black = superhumid periods, and dotted = dry periods.

sessions with 2–3 persons lasting 2–3 hours near mid-day, totaling 84 field days. The sessions ended when more than 80% of individuals captured represented recaptures of marks already given or recorded on that day.

Butterflies were net-captured, numbered on the underside of the forewings (felt-tipped pen), and released. Wing wear (seven “age” classes), point of capture, sex, forewing length and food sources were recorded (all following Freitas 1993, 1996, and Rogner & Freitas 1999). Forewing length was measured with a ruler, to the nearest mm. The age of individual butterflies was estimated in seven categories based on wing wear (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973), posteriorly grouped into three: new, intermediate and old (as in Freitas 1993, 1996 and Rogner & Freitas 1999). Values from one to seven, attributed to each wing wear class (where 1 = teneral and 7 = tattered) were used to compare the mean “age” of first captures in the different

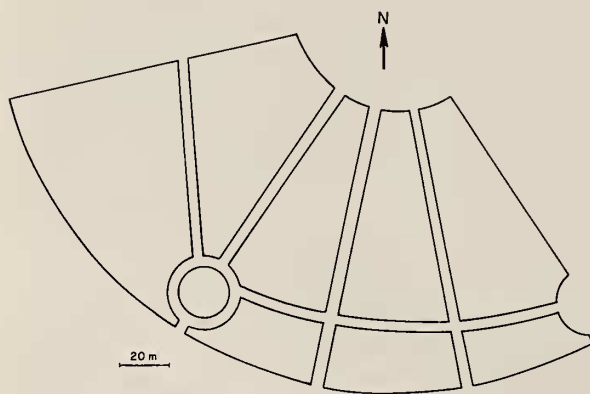


FIG. 2. Study area on the Campus of the Universidade Estadual de Campinas, showing the eight grassy areas (closed figures) separated by open trails. The small circular area, covered by dense shrubs (*Calliandra* sp., Fabaceae) was not sampled.

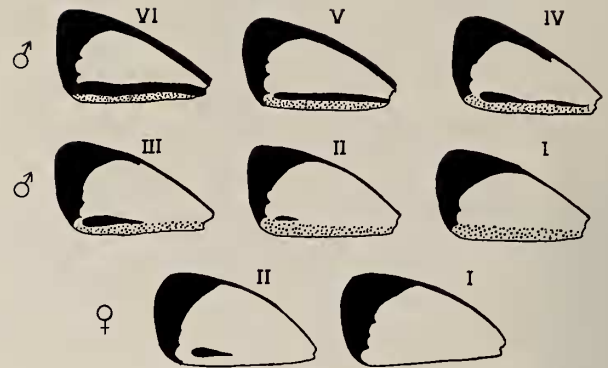


FIG. 3. Color types for males (top and middle rows) and females (bottom row) of *Eurema elathea* (background pale yellow, solid = black, dotted = orange).

color types. The amount of black on the dorsal forewing inner margin was recorded for males and females (details in next section).

The mark-release-recapture (MRR) data were analyzed by the Jolly-Seber (Southwood 1971) method for estimating population parameters (CMLR software developed by Dr. R. B. Francini, Unisantos) for the obtainment of estimated population numbers and standard errors. Daily results were tabulated as “number of individuals captured per day” (NICD), and “number of individuals present per day” (NIPD). To estimate the NIPD, recaptured individuals were considered to be present in the population on all previous days since the day of first capture (=marked animals at risk) (following Rogner & Freitas 1999). The data were grouped for analysis into “dry season” (May–August 1996) and “wet season” (September 1996–May 1997), in accord with the rainfall (climagram in Fig. 1).

Phenotype. Males were classified in six color types (I to VI) based on the amount of black on the dorsal forewing inner margin (Fig. 3), following a classification used previously by Ruszczyk and collaborators (unpublished data) for *E. elathea* in central Brazil. The extremes were “marginal black bar absent” (type I)

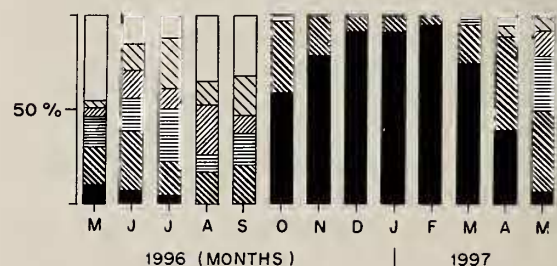


FIG. 4. Monthly percent of different male color types of *E. elathea* from May 1996 to May 1997. From top to bottom in first column, types I to VI.

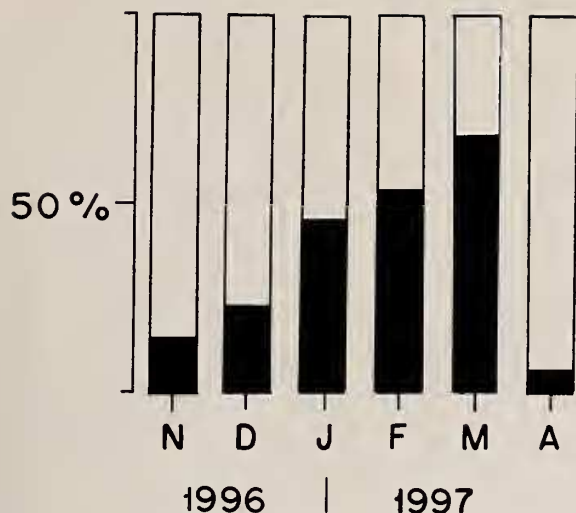


FIG. 5. Monthly percent of different female color types of *E. elathea* from May 1996 to May 1997. White = type I (pale), black = type II (dark). Because the type II was absent from May to October 1996, the first six months were combined in a single bar.

and “broad and complete marginal black bar” (type VI). In females only two color types were defined: “marginal black bar absent” (type I) and “short marginal black bar” (type II). Intermediates, as defined by the length and width of the black stripe, were not observed in females. The variation appeared to be continuous in males, causing some problems in defining the classes of intermediates especially in the first month (the first 40 individuals marked were discarded), resulting in a total number of assigned polyphenic types different from the total by sex.

RESULTS

Phenotype. Males of the color types I to IV were more common in the dry season, and V and VI were more common in wet season. The latter two phenotypes (dark forms) represented 90–100% of the total individuals seen in seven months (all in the wet season), and less than 50% in the other months (two in the wet season and all dry season months) (Fig. 4). Females of the color type II (the dark wet season form) appeared first in November 1996, disappearing after April 1997 (Fig. 5). The proportions should be compared with the climate of the previous month, when the individual completed larval growth and pupated. Thus, although September was a wet month, the proportion of lighter forms was very high, reflecting the dry weather of August; and even though April was relatively dry, the darker forms still predominated (Fig. 1).

Population biology. In all, 1468 individuals of *Eurema elathea* were captured during the 12 months of

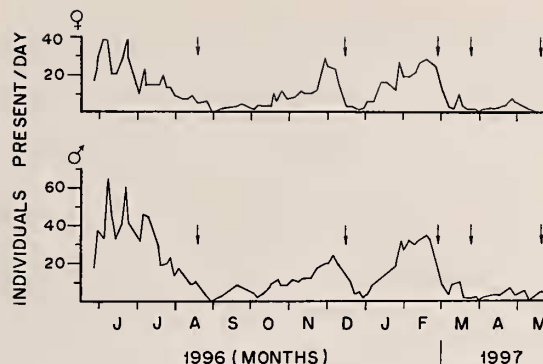


FIG. 6. Number of individuals present per day (NIPD) of males (below) and females (above) of *E. elathea* from May 1996 to May 1997. Arrows indicate mechanized grasscuttings.

the study, with 320 of these recaptured at least once. In the dry season (25 days), the number of individuals captured per day varied from 0 to 53 individuals (mean = 21.3; SD = 14.3) for males and 0 to 32 (mean = 13.6; SD = 8.2) for females. In the wet season (59 days), the number of individuals captured per day varied from 0 to 32 individuals (mean = 9.8; SD = 8.4) for males and 0 to 27 (mean = 7.9; SD = 7.8) for females. The number of individuals present per day in the dry season varied from 0 to 64 individuals (mean = 27.9; SD = 17.2) for males and 0 to 39 (mean = 17.6; SD = 11.0) for females. In the wet season, the same varied from 0 to 35 individuals (mean = 11.0; SD = 9.6) for males and 0 to 29 (mean = 8.7; SD = 8.7) for females. The population (based on NIPD) presented three peaks of abundance for both sexes: June–July 1996, November–December 1996 and February 1997 (Fig. 6). Mechanized grasscuttings (17 Aug. 1996, 13 Dec. 1996, 27 Feb. 1997, 23 Mar. 1997 and 17 May 1997, arrows in Fig. 6), led to decrease in adult abundance especially in 1997 after three grasscuttings at 24 and 55-day intervals.

Males were recaptured up to six times in the dry season and up to four times in the wet season; females were recaptured up to four times in dry season and up to three times in wet season. In all, 200 males and 120 females were recaptured at least once (Table 1). The highest recapture rate was observed in male color type I (dry season), and the lowest in male color type VI (wet season) and in both female color types (Table 2). Multiple recaptures were significantly more frequent in males (Table 2). The results of Jolly-Seber analysis for males and females separately (Figs. 7 and 8) show patterns very similar to those of NIPD (Fig. 6).

The total sex ratio (809 males and 659 females) was male biased ($\chi^2 = 15.3$, $df = 1$, $p < 0.001$), but when

TABLE 1. Recapture rates of adults of *Eurema elathea* in the study. cap = total captured, recap = individuals captured at least once. Asterisks on the Chi square values indicate that the difference is significant ($P < 0.05$, $df = 1$). Chi squares were calculated considering "cap" versus "individuals never recaptured" ("cap" minus "recap").

Sex	Dry		Wet		Total	
	cap/recap	%	cap/recap	%	cap/recap	%
Males	370/104	28.1	439/96	21.9	809/200	24.7
Females	265/59	22.3	394/61	15.5	659/120	18.2
Total	635/163	25.7	833/157	18.8	1468/320	21.8
Chi squares						
males vs females	$\chi^2 = 2.78$		$\chi^2 = 5.39^*$		$\chi^2 = 9.03^*$	
dry vs wet	$\chi^2 = 9.27^*$					

the months were analyzed separately, significant bias was observed in only four months (June, July and December 1996, and May 1997), with females dominating only in one month and sex ratio nearly 1:1 in four months (Fig. 9). Although the proportion of recaptures of males was higher than females, differences were significant only in the wet season, with total recapture rate significantly less than in the dry season (Table 1).

Age structure and residence time. Most of the first captures of both sexes were individuals of "intermediate" age (49% of males and 52% of females). Based on the categories of wing wear, the "age" of first recapture of males (mean class = 2.65, SD = 0.86, $n = 744$) was lower than females (mean = 2.83, SD = 0.87, $n = 660$) ($t = 4.0$, $df = 1402$, $p < 0.0001$). Color type VI was captured at a lower "age" than all other types except I (Table 2). The population showed peaks in abundance of "new" individuals in late June, Au-

TABLE 2. Population parameters of the different color types of *Eurema elathea*. Different superscript letters show significant differences among the different phenotypes. AFC = mean age at first capture (based on age categories), MRT = mean residence time (days), MUR = proportion of individuals with multiple recaptures (%), MOV = proportion of individuals that moved to another subarea (%).

	Males					Females		
	I	II	III	IV	V	VI	I	II
Marked	64	62	47	70	146	355	529	131
Recaptured	24	14	12	19	40	76	95	25
% of								
recapture*	37.5 ^a	22.6 ^{ab}	25.5 ^{ab}	27.1 ^{ab}	27.4 ^{ab}	21.4 ^b	17.9 ^b	19.1 ^b
AFC**	2.77 ^{ab}	2.86 ^a	2.89 ^a	2.78 ^a	2.89 ^a	2.43 ^b	2.77 ^a	2.85 ^a
MRT								
(days)***	11.4 ^a	10.5 ^a	8.6 ^a	12.0 ^a	9.0 ^a	10.2 ^a	7.5 ^a	9.1 ^a
MUR	45.8	35.7	25.0	52.6	35.0	32.9	21.0	16.0
MOV	83.3	57.1	75.0	73.7	80.0	75.0	61.0	76.0

* $p < 0.05$, Chi-square tests

** $p < 0.05$, one way ANOVA

*** $p > 0.05$, one way ANOVA

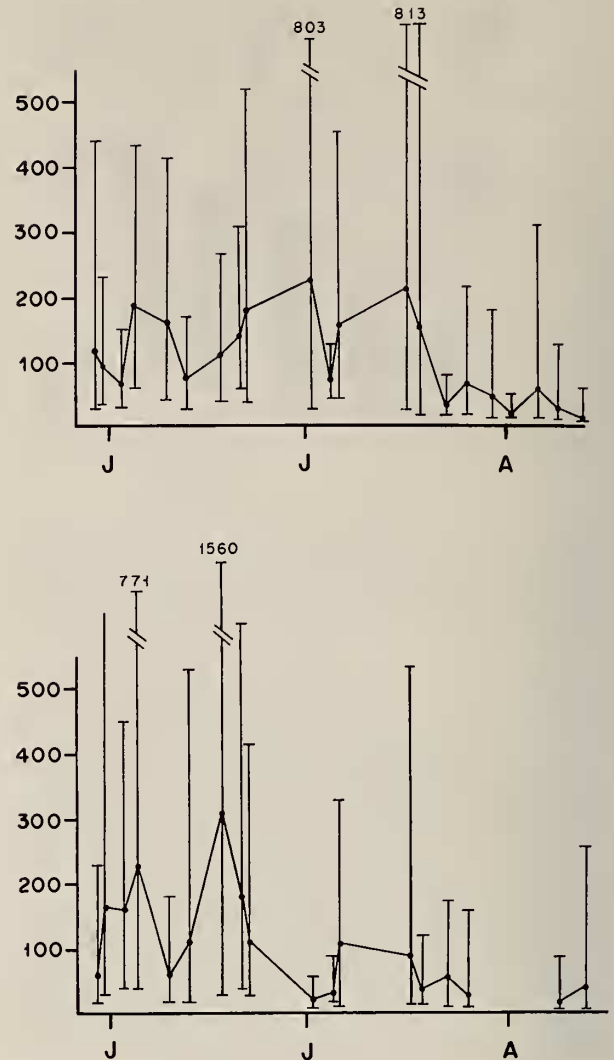


FIG. 7. Estimated population size (Jolly-Seber) for *E. elathea* males (above) and females (below), from May to August 1996. The maximum number of individuals is given as the estimate plus the error (superior part of vertical bars), and the minimum number is given as the number of individuals present per day (inferior part of vertical bars), assuming that the population could not be lower than this number.

gust–September, late November and February, suggesting high rates of recruitment in these periods (Fig. 10), with some indication of protandry.

Combining both seasons, residence time of males (mean = 9.8 days, SD = 7.7, $n = 201$) was not significantly higher than that of females (mean = 8.3 days, SD = 7.6, $n = 119$) ($t = 1.710$, $df = 318$, $p = 0.09$). However, differences were significant in the wet season ($t = 2.127$, $df = 155$, $p = 0.03$), and not in the dry season ($t = 0.749$, $df = 161$, $p = 0.45$). Residence times were marginally higher in the dry season for both males ($t = 1.95$, $df = 199$, $p = 0.052$) and females ($t =$

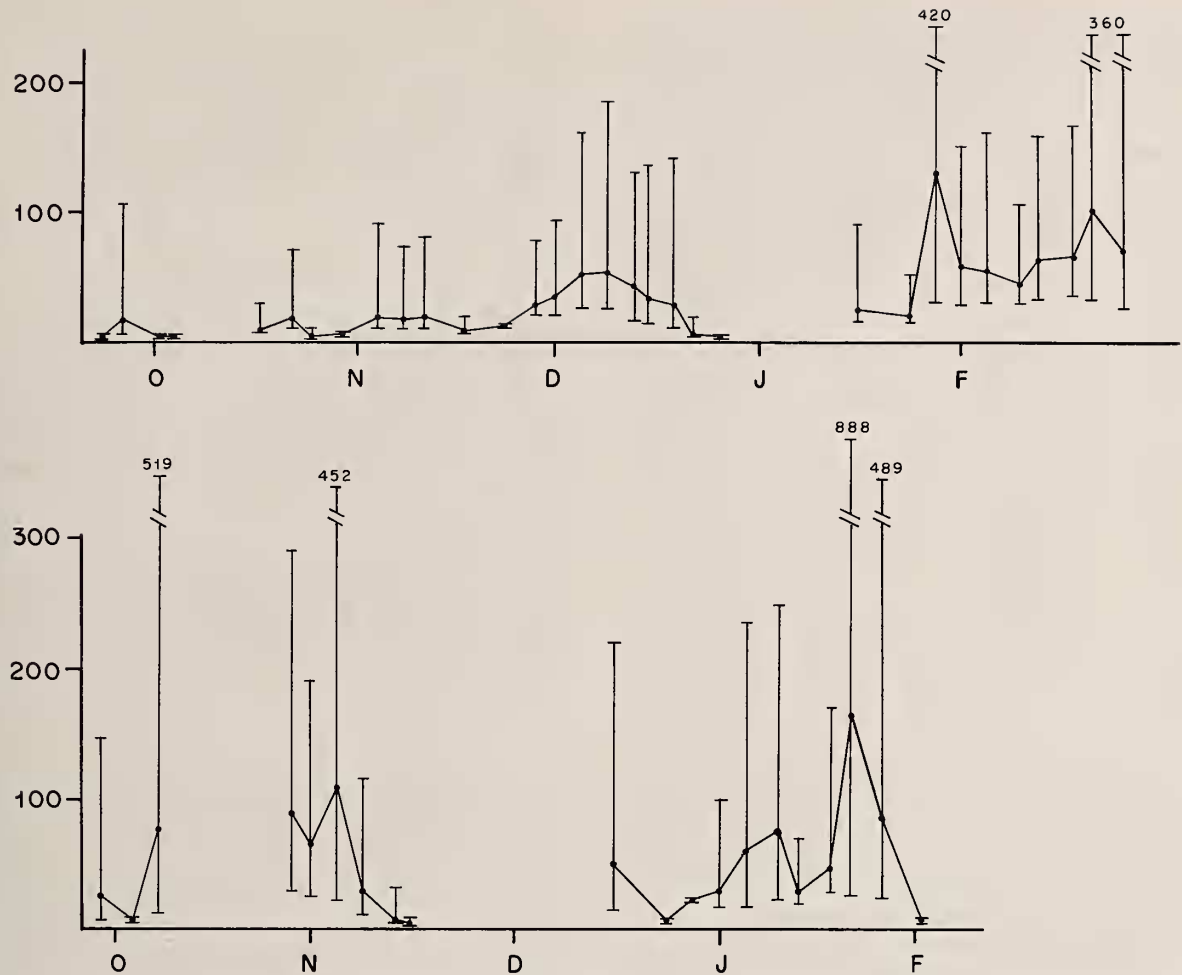


FIG. 8. Estimated population size (Jolly-Seber) for *E. elathea* males (above) and females (below), September 1996 to February 1997 (see Fig. 7 legend).

1.99, $df = 117$, $p = 0.049$) (see also Table 3). The maximum residence time in the dry season was 52 days for a male and 54 days for a female, and in the wet season 28 days for a male and 21 days for a female. The residence times were not different among the different phenotypes of males and females ($F_{7,297} = 0.903$, $p = 0.504$) (Table 2). Survival of males and females in each

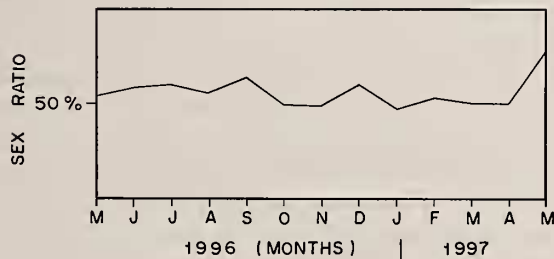


FIG. 9. Sex ratio for *E. elathea* from May 1996 to May 1997, as percent of males in each day's captures.

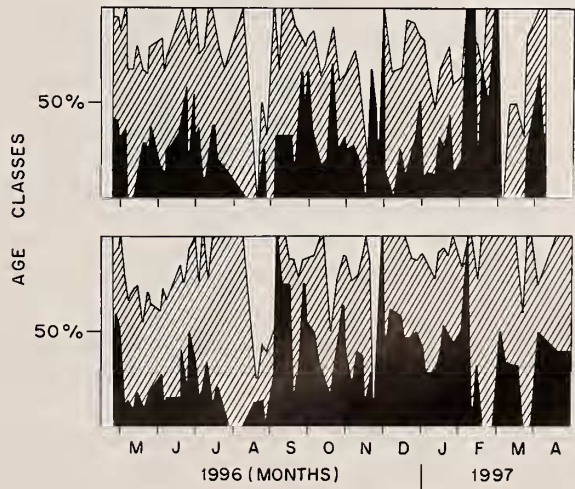


FIG. 10. Age structure of males (below) and females (above) of *E. elathea* (black = fresh individuals, hatched = intermediate, white = worn individuals) from May 1996 to May 1997.

TABLE 3. Residence time (in days) of *Eurema elathea* adults in the dry and wet seasons. Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP (days)	Males (%)	Females (%)	Total (%)
Dry Season			
1-5	36 (34.6)	29 (49.1)	65 (39.9)
6-10	23 (22.1)	12 (20.3)	35 (21.5)
11-15	22 (21.1)	5 (8.5)	27 (16.5)
16-20	8 (7.7)	4 (6.8)	12 (7.4)
21-25	8 (7.7)	4 (6.8)	12 (7.4)
26-30	2 (1.9)	4 (6.8)	6 (3.7)
31-35	3 (2.9)	—	3 (1.8)
> 35	2 (1.9)	1 (1.7)	3 (1.8)
Total	104	59	163 (100)
Mean \pm sd	10.9 \pm 9.1	9.7 \pm 9.8	
Max	52	54	
Wet Season			
1-5	34 (35.4)	32 (52.4)	66 (42.0)
6-10	33 (34.4)	15 (24.6)	48 (30.6)
11-15	16 (16.7)	11 (18.0)	27 (17.2)
16-20	9 (9.4)	2 (3.3)	11 (7.0)
21-25	2 (2.1)	1 (1.6)	3 (1.9)
26-30	2 (2.1)	—	2 (1.3)
Total	96	61	157 (100)
Mean \pm sd	8.8 \pm 5.6	6.9 \pm 4.2	
Max	28	21	

season are somewhat different (Table 3), with estimated median residence time ("life expectancy" of Cook et al. 1967) of 5.53 days for males and 4.72 days for females in the dry season, and 4.95 days for males and 4.87 days for females in the wet season.

Forewing length. For the entire sample, the average forewing length of females (mean = 17.9 mm, SD = 1.19, $n = 661$) was statistically greater than males (mean = 17.4 mm, SD = 1.05, $n = 782$) ($t = 7.51$, $df = 1441$, $p < 0.001$), and this difference was significant in seven months (Table 4). No significant differences in wing length were observed among the different color

TABLE 4. Mean forewing length (\pm SD) of *Eurema elathea* in this study. Asterisks indicates that means are different between sexes in that month (t -tests, $p < 0.05$). N = sample size.

Month/year	Males	N	Females	N
May/1996*	17.6 \pm 0.9	60	18.4 \pm 1.2	52
Jun/1996*	17.4 \pm 1.1	147	17.9 \pm 1.1	108
Jul/1996*	17.3 \pm 1.1	111	17.9 \pm 1.3	72
Aug/1996	17.2 \pm 1.4	32	17.8 \pm 1.3	32
Sep/1996	17.8 \pm 1.1	19	18.1 \pm 1.4	11
Oct/1996*	16.7 \pm 0.9	39	17.3 \pm 1.0	38
Nov/1996*	17.1 \pm 1.1	60	17.5 \pm 1.1	62
Dec/1996*	17.3 \pm 0.8	58	17.9 \pm 1.2	40
Jan/1997*	17.3 \pm 0.9	65	17.9 \pm 1.2	74
Feb/1997	17.7 \pm 0.9	133	17.8 \pm 1.2	120
Mar/1997	17.8 \pm 0.8	24	18.0 \pm 1.2	25
Apr/1997	17.8 \pm 0.9	20	17.9 \pm 1.1	23
May/1997	17.5 \pm 1.2	14	17.0 \pm 1.4	4

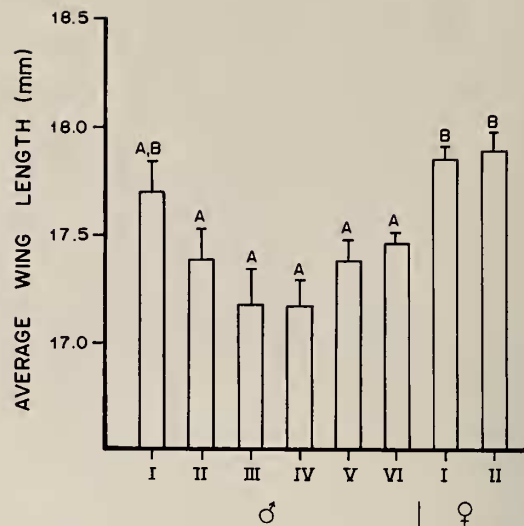


FIG. 11. Mean (\pm SD) forewing length of males and females of *E. elathea* (based on monthly recruitment). Different letters above the bars indicate significant differences in the means (one way ANOVA, $p < 0.005$).

types within sexes (Fig. 11). Average wing length of males was equal in the dry (mean = 17.4 mm, SD = 1.11, $n = 350$) and the wet season (mean = 17.4 mm, SD = 0.99, $n = 432$) ($t = 0.942$, SD = 780 $p = 0.34$). In females, average wing length in the dry season (mean = 18.0 mm, SD = 1.21, $n = 264$) was considered greater than in the wet season (mean = 17.8 mm, SD = 1.17, $n = 397$) ($t = -2.437$, $df = 659$, $p = 0.015$).

Natural history of the adults. Adults started activity around 0800 h in summer and 1000 h in winter, varying greatly with the weather (on some cold days during winter, the activity only began after 1100 h). As a rule, the peak of activity of the adults was between 1200 h and 1400 h, especially in the wet season, when many individuals were in courtship behavior or mating, and females usually were looking for plants for oviposition. After 1600 h, activity diminished, and especially in the dry season, the butterflies congregated in some grass patches in the study area to roost in loose aggregations.

Movements among the subareas were observed in all color types of both sexes. Males of color types I and V had the greatest number of individuals moving between sub-areas (Table 2). In the dry season, butterflies appeared to be more resident, engaging mainly in short flights, while in the wet season they were more active and frequently observed in long flights. Due to the fact that the different subareas were of unequal size, the proportions of individuals moving to other subareas do not reflect the flight distances.

Adults were usually seen feeding on flowers. Thirteen species of flowers were used as nectar sources. The most visited was *Emilia sonchifolia* (Asteraceae) (103 of a total of 150 records), but virtually any plant species in blossom was observed being used by the adults (see Oliveira 1996 for a list of flowers used in this same area).

DISCUSSION

Population biology. Male biased sex ratios have been observed in many natural populations of butterflies, even when the sex ratio in laboratory was 1:1 (e.g., Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973, Brussard et al. 1974, Watt et al. 1977, 1979, Brown & Ehrlich 1980, Ehrlich 1984, Ehrlich et al. 1984, Matsumoto 1984, 1985, Freitas 1993, 1996). Behavioral differences may contribute to this bias (Ehrlich 1984, Freitas 1996); Shapiro (1970) argues, however, that in several pierids this bias is related to the density of males. In this study, females accounted for 44.9% of the 1468 individuals collected in one year (male:female ratio 1.2:1), but the ratio was different from 1:1 in only four months.

Residence time of *E. elathea* is not high if compared to tropical butterflies in the genus *Heliconius* (Turner 1971, Benson 1972, Ehrlich & Gilbert 1973), but is similar to that obtained for some Ithomiinae (Vasconcellos-Neto 1980, Freitas 1993, 1996, Rogner & Freitas 1999). Dispersal of adults probably affects residence time, explaining the lower time of residence, mainly in the wet season. Especially the lower residence time of females in the wet season could be related to higher dispersal rates in this sex (see also Shapiro 1970 and Freitas 1993, 1996). Increased dispersal after the first rains has been reported in Ithomiinae in tropical seasonal forests (Vasconcellos-Neto 1980).

Also contrasting with populations of *Heliconius* butterflies, that maintain relatively constant numbers throughout the year (Turner 1971, Ehrlich & Gilbert 1973, Araujo 1980, Rogner & Freitas 1999), *E. elathea* fluctuated markedly in abundance throughout the year, in a way similar to that observed in Ithomiinae (Nymphalidae) and Troidini (Papilionidae) (Brown & Benson 1974, Drummond 1976, Haber 1978, Young & Moffett 1979, Vasconcellos-Neto 1980, 1986, 1991, Brown et al. 1981, Freitas 1993, 1996). Such fluctuations may be common in populations of temperate-zone pierids (Watt et al. 1977, 1979, Tabashnik 1980). For *E. elathea* in this study, these fluctuations are in part related to local grasscuttings, which probably destroyed many immatures, and made the adults leave the area looking for food sources. In the present work,

grasscuttings occurred in periods of population decline, on all occasions (Fig. 6), affecting the population and leading to very low numbers of butterflies in May 1997. Recolonization of the area probably occurred by individuals arriving from nearby populations, and the increase in the frequency of intermediate and old individuals after the first grasscutting (on 17 August 1996) supports this idea. The high proportion of first captures of individuals classified as intermediate and old suggests that migration might be common among subpopulations, and could provide new stock to a recently cut site. These population features suggest that this butterfly species would persist in metapopulations (Hanski & Gilpin 1997) in the study area. Further investigation on this subject could reveal important patterns in the ecology of butterflies in urban environments, but the results suggest that grasscuttings should be done after the first rains, when the population starts to be more vagile. Also, the grasscuttings in the dry season destroyed the roosting places of the butterflies, that could affect the survival of the individuals in the dry environment.

Even if reproductive diapause was not investigated in the present study, some comparisons can be made with other butterfly species in the seasonal tropics. Several species of tropical butterflies are known to exhibit reproductive seasonality (e.g., Jones & Rienks 1987, Braby 1995), and this pattern is supposed to be linked with rainfall, and consequently with the availability of host plants (Braby 1995). The pattern observed in *E. elathea* in the present study is similar to that exhibited by *E. hecabe* in Australia (Jones & Rienks 1987), with the maximum populational density reached in the middle of the dry season (but the effects of lawn mowing, that is affecting the population numbers, cannot be discarded). In *E. hecabe*, "gravid" females were present in all samples, but the proportion of them dropped when the population reached a peak (Jones & Rienks 1987). Thus, we could hypothesize that if *E. elathea* follows the same pattern, the population of this species present continuous breeding, but the number of reproductive females in the dry season (also the population peak) might be low. This subject is now under investigation by Rusczyk and collaborators in a population in central Brazil.

Polyphenism. In most studies of polyphenic species of butterflies, dry-season phenotypes were lighter and less conspicuous than wet-season phenotypes (Brakefield & Larsen 1984, Shapiro 1984, Brakefield 1987, Brakefield & Reitsma 1991, Jones 1992, Braby 1994, Windig et al. 1994). These differences have been related to ventral surface camouflage in the more sedentary color morphs produced in the dry sea-

son (Shapiro 1976, Brakefield & Larsen 1984, Brakefield & Reitsma 1991, Jones 1992, Van Dyck et al. 1997). In the present study, paler phenotypes were also more frequent in the dry season, when a brown substrate of dead leaves predominated on the ground where the butterflies rest. This paler phenotype may enhance survival of *E. elathea* through crypsis as the environment dries out and changes color (Owen 1971, Jones 1987, 1992). Thus, the different phenotypes could represent responses to seasonal differences in the environment and selective pressures such as predation (Brakefield & Larsen 1984, Brakefield 1987, Brakefield & Reitsma 1991). Braby (1994) proposed that in satyrs, dark wet-season forms rely on anti-predator devices (prominent eyespot patterns) which are displayed at rest and function to deflect attacks; while lighter dry-season forms with reduced eyespots probably rely on crypsis for survival. Windig et al. (1994) proposed that selection on males tends to favor wing patterns contributing positively to mate-seeking activity and thermal budgets (small and dark wings), while selection on females tends to favor paler ground colors and, in wet season forms, conspicuous markings (as female type II in this study). Allied with differences in color and pattern, differences in behavior in different seasons and phenotypes were observed on several occasions (Guppy 1986, Shreeve 1987, Nakasuji & Nakano 1990, Van Dyck et al. 1997). A possible hypothesis to be tested in tropical seasonal environments is that paler dry-season forms would be more resident than darker wet-season forms, that could enhance the value of their cryptic coloration (as reported in Van Dyck et al. 1997). The results of recapture rates of males of different color types of *E. elathea* in this study agree with this, since the paler color type (type I) had a higher recapture rate, and the darker color type (type VI) had a lower recapture rate (see Table 2). Unfortunately, the present study does not provide real distances traveled by the individuals, due to the fact that the different subareas were of unequal size (Fig. 2), and the hypothesis that paler phenotypes are more resident could not be tested.

Behavioral differences among the different color types could also be related to wing melanization (and, consequently, to thermoregulation) and body size (wing length). Van Dyck et al. (1997) hypothesize that small phenotypic wing differences could result in considerable variation in thermoregulation: darker butterflies could heat up more rapidly (Wasserthal 1975), and could spend more time flying and searching for females. In the study area, the wet season is also the warm season, and dark butterflies probably would become warm faster than pale forms, resulting in in-

creased flight activity. This could be true in many tropical seasonal habitats. If this holds, dark butterflies would benefit in all seasons (warm or cool), and their absence or low numbers in the dry season would be explained only by the cryptic advantage of the paler forms in dry season. Future research in this subject is needed to investigate this point.

The ventral pattern of the wings (not analyzed in this study) varies continually from plain white (mostly in the wet season) to patterned yellow and orange (mostly in the dry season) in both sexes. This is the side normally displayed by the butterflies at rest; the variation probably enhances camouflage and thermal effects in the different color types. Ruzsarczyk (pers. comm.) proposed that when *E. elathea* males are flying, the black bar of the darker types resembles the black bar of the hindwing outer margin of the distasteful moth *Utetheisa ornatatrix* (Arctiidae). The white pattern of the underside of these morphs also matches the light coloration of this moth. The two species often fly together and use similar substrates when perched, and this could be a good hypothesis to be investigated in the future.

Size is also important, since larger butterflies could more easily attain and maintain higher temperatures (Willmer & Unwin 1981). Van Dyck et al. (1997) propose that larger darker individuals would be adapted for patrolling and dispersal. Dry-season forms are in general larger than wet-season forms (Brakefield 1987, Brakefield & Reitsma 1991, Jones 1992, Braby 1994). Brakefield and Reitsma (1991) argue that this difference could be the result of behavioral and life history components: larger butterflies were the result of opportunistic development at the end of the wet season, while dry season forms derived more benefit from fast development (resulting in smaller size) which enables their progeny to complete development before the vegetation dries out. In most pierids, larger adults arise when larvae are reared at lower temperatures, and in two *Eurema* species larger size was induced by short photoperiods (Jones 1992). In this study, no significant differences in size in *E. elathea* were observed within the different color types, but the dry season females were larger than wet season females (not wet season forms). According to Braby (1994), several advantages could be associated with this increase in size, like increased longevity and capacity of storage in the fat body, both important in the dry season, when food resources are scarce.

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LITERATURE CITED

- ARAÚJO, A. M. 1980. Estudos genéticos e ecológicos em *Heliconius erato* (Lepidoptera, Nymphalidae). Actas do IV Congr. Latinoam. Genética, Vol 2:199–206.
- BENSON, W. W. 1972. Natural selection for Müllerian mimicry in *Heliconius erato* in Costa Rica. Science 176:936–939.
- BRABY, M. F. 1994. Phenotypic variation in adult *Mycalopsis* Hübner (Lepidoptera: Nymphalidae: Satyrinae) from the Australian wet-dry tropics. J. Aust. Ent. Soc. 33: 327–336.
- . 1995. Reproductive seasonality in tropical satyrine butterflies: strategies for the dry season. Ecol. Entomol. 20: 5–17.
- BRAKEFIELD, P. M. 1987. Tropical dry and wet season polyphenism in the butterfly *Melanitis leda* (Satyrinae): phenotypic plasticity and climate correlates. Biol. J. Linn. Soc. 31: 175–191.
- BRAKEFIELD, P. M. & T. B. LARSEN. 1984. The evolutionary significance of dry and wet season forms in some tropical butterflies. Biol. J. Linn. Soc. 22: 1–12.
- BRAKEFIELD, P. M. & N. REITSMA. 1991. Phenotypic plasticity, seasonal climate and the population biology of *Bicyclus* butterflies (Satyridae) in Malawi. Ecol. Entomol. 16: 291–303.
- BROWN, I. L. & P. R. EHRLICH. 1980. Population biology of the checkerspot butterfly, *Euphydryas chalcedona*. Structure of the Jasper Ridge colony. Oecologia 47: 239–251.
- BROWN, K. S. JR. 1992. Borboletas da Serra do Japi: Diversidade, habitats, recursos alimentares e variação temporal, pp. 142–187, 18 figs. In L. P. C. Morellato, (ed.), História natural da Serra do Japi. Ecologia e preservação de uma área florestal no sudeste do Brasil. Campinas, Editora da Unicamp/Fapesp.
- BROWN, K. S. JR. & W. W. BENSON. 1974. Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepid. Nymph.). Biotropica 6(4): 205–228.
- BROWN, K. S. JR., A. J. DAMMAN & P. P. FEENY. 1981. Troidine swallowtails (Lepidoptera: Papilionidae) in Southeastern Brazil: Natural history and foodplant relationships. J. Res. Lepid. 19(4): 199–226.
- BRUSSARD, P. F. & P. R. EHRLICH. 1970. The population structure of *Erebia epipsodea* (Lepidoptera: Satyrinae). Ecology 51: 119–129.
- BRUSSARD, P. F., P. R. EHRLICH & M. C. SINGER. 1974. Adult movements and population structure in *Euphydryas editha*. Evolution 28: 408–415.
- CHEW, F. S. 1995. From weeds to crops: changing habitats of pierid butterflies (Lepidoptera: Pieridae). J. Lepid. Soc. 49(4): 285–303.
- COOK, L. M., L. P. BROWER & H. J. CROZE. 1967. The accuracy of a population estimation from multiple recapture data. J. Anim. Ecol. 36: 57–60.
- DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, Nymphalidae. Princeton Univ. Pr. 327 pp, 51 pl.
- DRUMMOND, B. A. III. 1976. Comparative ecology and mimetic relationships of ithomiine butterflies in eastern Ecuador. Ph.D. Thesis, University of Florida, Gainesville, USA, xvi + 361 pp.
- EHRLICH, P. R. 1984. The structure and dynamics of butterfly populations, pp. 25–40. In R. I. Vane-Wright, & P. R. Ackery (eds.), The biology of butterflies. Academic Press, London.
- EHRLICH, P. R. & S. E. DAVIDSON. 1960. Techniques for capture-recapture studies of Lepidoptera populations. J. Lepid. Soc. 14: 227–229.
- EHRLICH, P. R. & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5: 69–82.
- EHRLICH, P. R., A. E. LAUNER & D. D. MURPHY. 1984. Can sex ratio be defined or determined? The case of a population of checkerspot butterflies. Am. Nat. 124(4): 527–539.
- FREITAS, A. V. L. 1993. Biology and population dynamics of *Placidula euryanassa*, a relict ithomiine butterfly (Nymphalidae: Ithomiinae). J. Lepid. Soc. 47: 87–105.
- . 1996. Population biology of *Heterosais edessa* (Nymphalidae) and its associated Atlantic Forest Ithomiinae community. J. Lepid. Soc. 50: 273–289.
- GUPPY, C. S. 1986. The adaptive significance of alpine melanism in the butterfly *Parnassius phoebus* F. (Lepidoptera: Papilionidae). Oecologia 70: 205–213.
- HABER, W. 1978. Evolutionary ecology of tropical mimetic butterflies (Lepidoptera: Ithomiinae). Ph.D. Dissertation, Univ. of Minnesota, Minneapolis, Minnesota, USA, xii + 227 pp.
- HANSKI, I. & M. E. GILPIN. 1997. Metapopulation dynamics: ecology, genetics and evolution. Academic Press, London.
- JONES, R. E. 1987. Reproductive strategies for the seasonal tropics. Insect Sci. Applic. 8: 515–521.
- . 1992. Phenotypic variation in Australian *Eurema* species. Aust. J. Zool. 40: 371–383.
- JONES, R. E. & J. RIENKS. 1987. Reproductive seasonality in the tropical genus *Eurema* (Lepidoptera: Pieridae). Biotropica 19: 7–16.
- KINGSOLVER, J. G. & D. C. WIERNASZ. 1987. Dissecting correlated characters: adaptive aspects of phenotypic covariation in melanization pattern of *Pieris* butterflies. Evolution 41(3): 491–503.
- KINGSOLVER, J. G. & D. C. WIERNASZ. 1991. Seasonal polyphenism in wing-melanin pattern and thermoregulatory adaptation in *Pieris* butterflies. Am. Nat. 137: 816–830.
- MATSUMOTO, K. 1984. Population dynamics of *Luehdorfia japonica* Leech (Lepidoptera: Papilionidae). I. A preliminary study on the adult population. Res. Popul. Ecol. 26: 1–12.
- . 1985. Population dynamics of the Japanese Clouded Apollo *Parnassius glacialis* Butler (Lepidoptera: Papilionidae). I. Changes in population size and related population parameters for three successive generations. Res. Popul. Ecol. 27: 301–312.
- NAKASUJI, F. & A. NAKANO. 1990. Flight activity and oviposition characteristics of the seasonal form of a migrant skipper, *Parnara guttata guttata* (Lepidoptera: Hesperidae). Res. Popul. Ecol. 32: 227–233.
- NOSS, R. F. 1996. The naturalists are dying off. Conserv. Biol. 10 (1): 1–3.
- NYLIN, S. 1989. Effects of changing photoperiods in the life cycle regulation of the comma butterfly, *Polygonia c-album* (Nymphalidae). Ecol. Entomol. 14: 209–218.
- OLIVEIRA, L. J. 1996. Comportamento da borboleta *Eurema elathea*. An. Soc. Entomol. Brasil 25: 401–409.
- OWEN, D. F. 1971. Tropical butterflies: the ecology and behaviour of butterflies in the tropics with special reference to African species. Clarendon Press, Oxford.
- ROGNER, R. R. & A. V. L. FREITAS. 1999. Population biology, wing color variation and ecological plasticity in *Heliconius erato* phyllis (Nymphalidae). J. Lepid. Soc. 53: 11–21.
- SAALFELD, K. & A. M. ARAÚJO. 1981. Studies on the genetics and ecology of *Heliconius erato* (Lepid., Nymph.). I: Demography of a natural population. Rev. Bras. Biol. 41: 855–860.
- SANTOS, E. O. 1965. Cap. 4°—Características climáticas, pp. 95–150. In A. Baixada Santista. Aspectos Geográficos. Volume 1. As Bases Físicas. Editora da Universidade de São Paulo.
- SHAPIRO, A. M. 1970. The role of sexual behavior in density-related dispersal of pierid butterflies. Am. Nat. 104: 367–372.
- . 1976. Seasonal polyphenism. Evolutionary Biology 9: 259–333.
- . 1984. Polyphenism, phyletic evolution, and the structure of the pierid genome. J. Res. Lepid. 23: 177–195.
- SHREEVE, T. G. 1987. The mate location behavior of the male speckled wood butterfly, *Pararge aegeria*, and the effect of phenotypic differences on hind-wing spotting. Anim. Behav. 35: 682–690.

- SOUTHWOOD, T. R. E. 1971. Ecological methods with particular reference to the study of insect populations. Chapman & Hall, London. 524 p.
- TABASHNIK, B. E. 1980. Population structure of pierid butterflies. III. Pest populations of *Colias philodice eriphyle*. *Oecologia* 47: 175–183.
- TURNER, J. R. G. 1971. Experiments on the demography of tropical butterflies. II. Longevity and home range behavior in *Heliconius erato*. *Biotropica* 3(1): 21–31.
- VAN DYCK, H., E. MATTHYSEN & A. A. DHONDT. 1997. The effect of wing color on male behavioral strategies in the speckled wood butterfly. *Anim. Behav.* 53: 39–51.
- VASCONCELLOS-NETO, J. 1980. Dinâmica de populações de Ithomiinae (Lepidoptera: Nymphalidae) em Sumaré-SP. M.S. Thesis, Universidade Estadual de Campinas, Campinas, SP. vi + 206 pp.
- . 1986. Interactions between Ithomiinae (Lepidoptera: Nymphalidae) and Solanaceae, pp. 366–377. In W. G. D'Arcy, (ed.), *Solanaceae, biology and systematics*. Columbia University Press, New York. 603 pp.
- . 1991. Interactions between ithomiine butterflies and Solanaceae: feeding and reproductive strategies, pp. 291–313. In P. W. Price, T. M. Lewinsohn, G. W. Fernandes & W. W. Benson (eds.), *plant-animal interactions. Evolutionary ecology in tropical and temperate regions*. John Wiley & Sons, Inc., New York.
- WALTER, H. 1985. *Vegetation of the Earth*. Springer-Verlag, Berlin, Germany.
- WASSERTHAL, L. T. 1975. The role of butterfly wings in regulation of body temperature. *J. Insect Physiol.* 21: 1921–1930.
- WATT, W. B., F. S. CHEW, L. G. SNYDER, A. G. WATT & D. E. ROTH-SCHILD. 1977. Population structure of pierid butterflies. I. Numbers and movements of some montane *Colias* species. *Oecologia* 27: 1–22.
- WATT, W. B., D. HAN & B. TABASHNIK. 1979. Population structure of pierid butterflies. II. A "native" population of *Colias philodice eriphyle* in Colorado. *Oecologia* 44: 44–52.
- WILLMER, P. G. & D. M. UNWIN. 1981. Field analyses of insect heat budgets: reflectance, size and heating rates. *Oecologia* 50: 250–255.
- WINDIC, J. J., P. M. BRAKEFIELD, N. REITSMA & J. G. M. WILSON. 1994. Seasonal polyphenism in the wild: survey of wing pattern in five species of *Bicyclus* butterflies in Malawi. *Ecol. Entomol.* 19: 285–298.
- YOUNG, A. M. & M. W. MOFFETT. 1979. Studies on the population biology of the tropical butterfly *Mechanitis isthmia* in Costa Rica. *Amer. Midl. Nat.* 101: 309–319.

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